Predator Abundance in Alfalfa Fields in Relation to Aphids, Within-Field Vegetation, and Landscape Matrix

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ABSTRACT We used multiple regression modeling to investigate the numerical response by the predatory insects *Hippodamia convergens* Guérin-Méneville, *H. parenthesis* (Say), and *C. septempunctata* L. (Coleoptera: Coccinellidae), *Chrysoperla plorabunda* (Fitch) (Neuroptera: Chrysopidae), and *Nabis americoferus* Carayon (Hemiptera: Nabidae) to aphids during 5 yr in three geographically separated alfalfa fields in eastern South Dakota. Regression models for abundance of adults of all species were significant. Regression models for immature *H. convergens, H. parenthesis,* and *C. septempunctata* were significant, but regression models for immature *C. plorabunda* and *N. americoferus* were not significant. Regression parameters differed among the three fields for most predator species, indicating that the numerical response was dependent on geographical location. To obtain insight into why the numerical response by predators differed among fields we determined how the abundance of predators in alfalfa fields was influenced by the landscape surrounding a field and the vegetation in it. Variables describing the complexity of the landscape surrounding alfalfa fields and the plant community in the fields entered into regression models for predator abundance and explained a greater proportion of the variance in predator abundance than aphid abundance did. We conclude that the structure of the landscape matrix plays an important role in determining the abundance of aphid predators in alfalfa fields, as does the plant community in a field. These effects can sometimes overshadow the direct numerical response by predators to aphids.

KEY WORDS Coccinellidae, aphids, landscape structure, natural enemies, predator-prey interaction, alfalfa

Suppression of pest insects in agricultural crops by natural enemies is generally thought to be the result of direct density dependent processes such as the functional response whereby natural enemies increase their attack rate in response to increasing prey density, and the numerical response whereby natural enemies increase their reproduction in the field. Suppression may also involve a spatial aspect to the numerical response, whereby predators aggregate preferentially in areas where prey density is high (Readshaw 1973, Hassell 1978).

Several aphid predators, primarily Coccinellidae, Chrysopidae, and Nabidae, prey on aphids in alfalfa (Medicago sativa L.) fields in eastern South Dakota (Elliott and Kieckhefer 1990). Interest in these predators stems from the observation that they play an important role in keeping aphid densities low in alfalfa and some other field crops (Frazer et al. 1981, Kring et al. 1985, Rice and Wilde 1988). These predators obtain resources necessary for survival and reproduction from a variety of habitats. The resources include aphids, but also other requisites at various times during a species life cycle, such as appropriate microclimate for overwintering, which for Coccinellidae typically occurs in wooded or other seminatural habitats (Hodek and Honek 1996).

Characteristics of the habitat within an alfalfa field and in the landscape matrix within which the field is embedded might be expected to influence the number of predators that occur in the field. In particular, the plant community in a field, and the patchwork mosaic of plant communities in the landscape surrounding the field may be important to predator population dynamics (Landis et al. 2000). The presence of weeds in an agricultural field can influence the abundance and distribution of natural enemies the field, although the reasons for this are varied (Norris and Kogan 2000). Very little information exists on the importance of weeds in alfalfa fields to aphid predators. In one of the only published studies, Barney et al. (1984) found that

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nabids were more abundant in grass-infested alfalfa fields than in pure stands of alfalfa. The structure of the landscape matrix surrounding an agricultural field can also influence the number of natural enemies that occur in the field (Duelli et al. 1990, Thies and Tsharntke 1999). The landscape matrix probably affects natural enemy populations by rendering particular requisites of natural enemies more or less abundant and accessible (Menalled et al. 1999), and the magnitude of the effect is most likely related to a species dispersal ability and behavior (Dunning et al. 1992, Taylor et al. 1993). Species that differ with respect to resource requirements, behavior, and mobility will be affected differently when confronted with a particular spatial mosaic. Colunga-Garcia et al. (1997) found that the number of Coccinellidae species caught on sticky traps stationed in alfalfa fields was greater in fields embedded in a matrix of diverse patch types than in a less complex matrix; whereas Honek (1982) showed that landscape structure had a small, but measurable effect on coccinellid density in alfalfa fields in central Bohemia.

In light of previous studies we sought to obtain information on the numerical response by predators to aphids in alfalfa fields, and on whether plant communities within fields and in the surrounding landscape played a role in determining numbers of predators in alfalfa fields. We addressed three questions concerning the abundance of predators in alfalfa fields. First, do aphid predators exhibit a numerical response to variation in aphid density that occurs in individual fields? If so, there should be more predators in alfalfa fields when aphids are abundant than when they are not, and we would expect that regression models relating predator to aphid abundance would be significant. Based on previous studies (e.g., Neuenschwander et al. 1975, Frazer et al. 1981) we expected to answer the first question affirmatively. Second, is the numerical response by predators to aphids similar in geographically widely separated alfalfa fields? If the predators are distributed more or less uniformly in space, or if all fields are approximately equally accessible and attractive to the predators, parameters of regression models should be identical for geographically separated fields. However, if aphid predator numbers vary markedly in space, and predators respond strongly to spatially varying factors, we could find that regression parameters for geographically separated fields differ substantially. Finally, do features of the landscape matrix surrounding a field and those of the habitat within it affect the number of predators that inhabit alfalfa fields? If the answer to the second question is no, i.e., the numerical response by predators differs markedly among fields, is the plant community within the field and the mosaic of communities in the surrounding landscape important in determining the number of predators in the field? This question is relevant to assessing the potential for conserving aphid predators by habitat management.

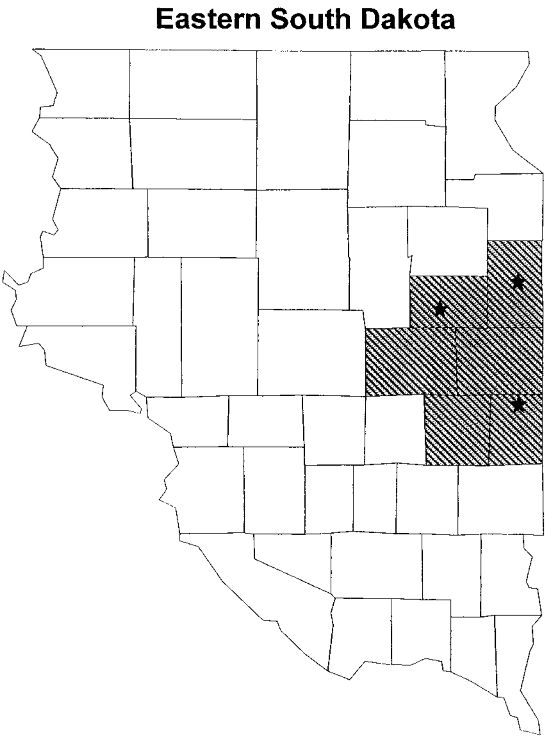

Fig. 1. Six-county study area in eastern South Dakota. Approximate locations of fields that were repeatedly sampled during 5 yr (1988–1992) are identified with stars.

Materials and Methods

Data Collection. *Study Fields.* The study was conducted in alfalfa fields in six eastern South Dakota counties: Brookings, Deuel, Hamlin, Kingsbury, Lake, and Moody (Fig. 1). All alfalfa fields selected for study had been planted to alfalfa for at least 1 yr before study.

To investigate patterns in abundance of aphid predators in relation to the abundance of aphids for geographically separated alfalfa fields, a single field in each of three counties (Moody, Hamlin, and Deuel) was sampled annually throughout the growing season each year from 1988 though 1992. Distances between the fields ranged from 50 to 80 km. The number of times a field was sampled during a growing season varied due to inclement weather and logistical constraints, and ranged from 4 to 10 (median = 7) samplings per field per year.

To investigate spatial patterns in abundance of aphid predators in relation to vegetation within fields and to landscape structure, a variable number of fields in the six counties was sampled during 1988, 1989, and 1990. These fields were chosen arbitrarily from within each county, and a particular field was sampled only one time during the study. We avoided sampling fields in close proximity so that the landscape matrix surrounding fields (defined below) would overlap minimally or not at all among study fields. All sampling was done between 1 July and 15 August of each year. In

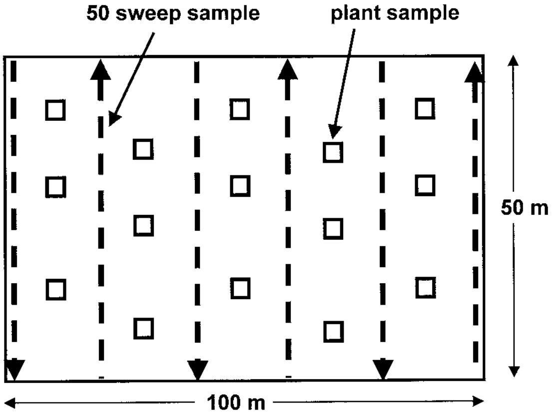

Fig. 2. Plot layout for insect and vegetation sampling within an alfalfa field.

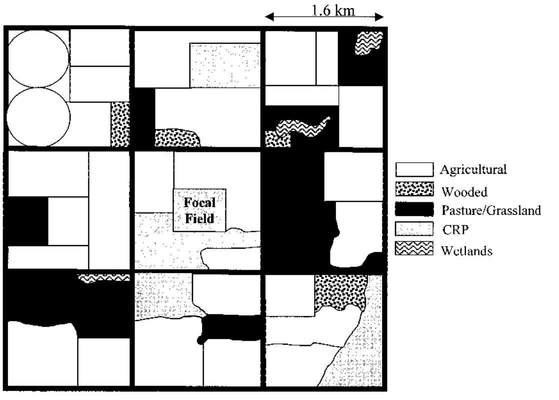

Fig. 3. Hypothetical study field and the surrounding landscape matrix.

total, 32, 35, and 45 alfalfa fields were sampled, respectively, in 1988, 1989, and 1990.

Insect and Vegetation Measurements. Each time a field was sampled, a single 50 by 100-m study plot was established at an arbitrary location in the field. The study plot was established at least 50 m from the field edge to avoid the potential for edge effects. For fields that were sampled multiple times during the growing season, the study plot was established at a new location each time the field was sampled. No attempt was made to ensure that the new study plot did not overlap a previous plot. Aphid predators (Coccinellidae, Nabidae, and Chrysopidae) and aphids were sampled in fields using a 38-cm-diameter sweepnet by taking six 50-sweep subsamples (total of 300 sweeps) along approximately equally spaced transects through the plot (Fig. 2). Ambient air temperature (°C), percent relative humidity, solar irradiance (w/m^2), and wind speed (m/s) were measured just before and just after sweepnet sampling. The number of each aphid predator species in a 50-sweep subsample was recorded. Aphid abundance was estimated for each 50-sweep subsample by assigning the number of aphids in the subsample to one of 15 categories. This was done as a practical necessity to reduce the time required to process samples. By this method, the number of aphids per 50-sweep subsample was assigned a number ranging from 0 to 12,288. If zero, one, or two aphids were present, the actual number of aphids in the subsample was assigned. For subsamples containing three or more aphids, the number was estimated as the midpoint of an interval defined by raising the number 2 to incrementally increasing integer powers. For example, if three or four aphids were present the number assigned was 3.5, if five to eight aphids were present the number assigned was 6.5, if nine to 16 aphids were present the number assigned was 12.5, and so on. The largest number of aphids observed in a 50-sweep subsample was between 8,192 and 16,384 and was assigned the value 12,288. The method saved considerable time when numerous aphids were present because the number to assign could be easily ascertained without actually counting the aphids.

Vegetation was measured in each plot using a systematic sampling method in which 15 measurements were taken at approximately equidistant locations in the plot (Fig. 2). Canopy coverage by alfalfa, herbaceous weeds, and grassy weeds was measured at each location. Canopy coverage measurements involved scoring the area of a 20 by 50-cm quadrat encompassed by the canopy of each plant group on a scale of 1–6 (Daubenmire 1959). The percentage of the quadrat covered by a particular category of vegetation was scored as follows: 1 = <5%, 2 = 5–25%, 3 = 26–50%, 4 = 51–75%, 5 = 76–95%, and 6 = >95% coverage. Alfalfa plant growth stage was measured by assigning a score of 1–5 to the stand in a field. A score of 1 indicated that plants were in the prebud stage, a score of 2 indicated bud stage, a score of 3 indicated that 1–10% of plants were flowering, a score of 4 indicated that 11–50% of plants were flowering, and a score of 5 indicated that >50% of plants were flowering. Plant canopy height was also measured at each location in the plot.

Landscape Measurements. The composition of the landscape surrounding each field was determined from high altitude aerial panchromatic photographs obtained from the U.S. Farm Service Agency, Brookings, SD. Land cover was grouped into five classes: cultivated, grassland/pasture, wooded, USDA Conservation Reserve Program (CRP), and wetlands/water. Land enrolled in the CRP is planted to grasses, but is not grazed, mowed, or burned. Land covered by artificial structures such as farmsteads and roads was not recorded. The number of hectares in each of the five land-cover categories was calculated for each of nine 1.6 by 1.6-km blocks centered on the block containing the sampled field (Fig. 3). These data were then expressed as the percentage of the total area of each block. The number of boundary crossings between land cover categories was estimated for each block by drawing two straight lines from corner to corner across the diagonals of the block and counting the number of boundaries crossed along the length of each line. We considered boundary density to be a measure of the patch size of the landscape. Shannon's patch diversity index was calculated and used to measure the diversity of land cover types (O'Neill et al. 1988). The mean of each landscape variable for the nine 1.6-km^2 blocks was calculated and used in subsequent regression modeling. The percentage of cultivated land was not included as a predictor variable in regression modeling because of its very strong correlation with the overall percentage of land in noncultivated land cover categories.

Data Analysis. *Aphid Effects on Predator Abundance.* Predator and aphid abundance data for the six subsamples taken from a field on a sampling occasion were averaged. To determine if a relationship existed between the abundance of a particular predator and the abundance of aphids, a regression model was fitted to all data collected from the three fields during the 5 yr. A regression model was constructed for each species of predator that was sufficiently abundant in samples to permit an adequate model to be constructed. To account for the possibility of numerical response curves with nonlinear structure, the square and cube of aphid abundance were calculated and used with aphid abundance as predictor variables in regression modeling. With quadratic and cubic predictor variables included it was possible to represent both linear numerical response functions, with a constant rate of increase in predator density as a function of prey density, but also to represent more complex relationships where the rate of increase in predator abundance depended on aphid abundance. For example, inclusion of the quadratic term would permit description of a numerical response where predator numbers increased with increasing prey density, but at a continuously decreasing rate. The possibility that numerical response functions differed between the three geographically separated fields was also considered in modeling. This was accomplished by including unique predictor variables for each location. Polynomial regression modeling was accomplished by stepwise regression using PROC REG (SAS Institute 1990). *F*-tests were used to determine the variables to include in each model, with the significance level for inclusion of a predictor variable set at $\alpha = 0.05$.

Vegetation and Landscape Effects on Predator Abundance. For purposes of multiple regression modeling, there were six landscape variables and four habitat variables (Table 1). We were interested in the effects on predator abundance of landscape composition and patchiness, and within field vegetation composition and aphid abundance. We were not interested in temporal variation in vegetation and aphids within fields. Therefore, alfalfa plant growth stage, year, day of the year, and time of day were used as covariables in regressions to adjust predictor variables that might vary temporally (canopy coverage by broadleaf weeds, grasses, and alfalfa, and aphid abundance) before using these variables to construct multiple regression models. If visual examination of the residuals of response variables regressed on a particular covariable indicated a nonlinear relationship, second order, and if necessary, higher order terms were added to the regression model until evidence of lack-of-fit disappeared. The adjusted predictor variables (actually residuals of the above mentioned regressions) were combined with landscape variables and used in constructing multiple regression models for predator abundance by stepwise regression. The square and cube of all predictor variables were also included as predictors to allow for the existence of nonlinear effects.

Table 1. Landscape, within-field habitat, and covariables recorded for alfalfa fields sampled for aphid predators during 1988, 1989, and 1990

Variable	Mean (range)
Habitat variables	
Aphid abundance	9.1 (0.2–3,070.7)
Alfalfa coverage	4.3 (2.5–6.0)
Broadleaf weed coverage	0.3 (0.0–2.1)
Grassy weed coverage	1.0 (0.0–3.8)
Landscape variables	
% grassland and pasture	18.3 (4.0–51.2)
% woods	3.2 (1.1–12.6)
% CRP	5.2 (0.0–33.7)
% wetlands and water	4.8 (0.0–36.2)
No. of boundaries crossed	6.8 (3.8–11.6)
Shannon's patch diversity index	2.4 (1.4–4.1)
Covariables	
Alfalfa plant height, cm	43.9 (21.6–69.3)
Alfalfa plant growth stage	2.45 (1.0–5.0)
Year	1989 (1988–1990)
Day of the year	204.5 (183–226)
Time of day (hours)	1235 (0900–1545)
Windspeed, m/sec	3.17 (0.07–8.47)
Air temp, °C	26.7 (18.9–35.6)
Relative humidity, %	56.1 (24–86)
Solar radiation, w/m^2	1,135 (135–1,600)

Covariables were used as independent variables to adjust predator abundance and within-field habitat variables for temporal variability.

Some meteorological variables, time of day, and plant canopy height are known to influence the efficiency of sweepnet sampling for some aphid predators in alfalfa (Elliott and Michels 1997). Furthermore, predator abundance varies seasonally (Elliott and Kieckhefer 1990). Therefore, as was done with predictor variables, response variables (predator abundance) were adjusted by forcing meteorological variables, alfalfa plant height, day of the year, and time of day into regression models before initiating the stepwise phase for variable inclusion, during which habitat and landscape variables were incorporated. As with predictor variables, residuals of regressions of predator abundance against covariables were examined and nonlinear terms were added if necessary to correct for lack-of-fit. For multiple regression models for predator abundance as a function of landscape variables, within-field vegetation, and aphid abundance, *F*-tests were used to determine the significance of predictor variables in regression models with $\alpha = 0.05$ for inclusion of a predictor in a model. Regression models were developed using PROC REG (SAS Institute 1990).

Results

Aphid Effects on Predator Abundance. The abundance of aphids and aphid predators fluctuated from

Table 2. The mean number of aphids per 50 sweeps (± SE) and mean number of aphid predators per 50 sweeps (± SE) for three alfalfa fields sampled each year for 5 yr (1988–1992)

Insect	Year					All Years
	1988 (17)	1989 (14)	1990 (27)	1991 (27)	1992 (17)	(102)
Aphids	1.27 ± 1.54	96.5 ± 1.93	81.3 ± 1.57	20.1 ± 1.43	27.8 ± 1.51	27.1 ± 1.27
Adult predators						
N. americoferus	5.86 ± 1.34	2.38 ± 0.42	4.86 ± 0.90	6.89 ± 1.18	7.94 ± 2.51	5.74 ± 0.63
C. plorabunda	0.43 ± 0.14	0.56 ± 0.26	1.31 ± 0.53	0.48 ± 0.24	0.38 ± 0.17	0.68 ± 0.16
H. convergens	1.41 ± 0.45	5.20 ± 1.79	0.19 ± 0.05	0.38 ± 0.20	2.02 ± 0.87	1.44 ± 0.33
H. parenthesis	0.86 ± 0.20	0.52 ± 0.09	0.26 ± 0.09	0.20 ± 0.06	0.04 ± 0.02	0.30 ± 0.05
C. septempunctata	0.09 ± 0.04	1.02 ± 0.18	0.72 ± 0.17	0.93 ± 0.26	0.88 ± 0.42	0.74 ± 0.11
other coccinellids	0.09 ± 0.02	0.07 ± 0.04	0.07 ± 0.03	1.13 ± 0.31	2.08 ± 0.82	0.69 ± 0.17
Larvae (or nymphs)						
N. americoferus	0.24 ± 0.11	0.50 ± 0.18	1.65 ± 0.53	1.31 ± 0.45	5.90 ± 2.73	1.88 ± 0.51
C. plorabunda	0.13 ± 0.08	0.62 ± 0.33	0.19 ± 0.10	0.08 ± 0.03	0.21 ± 0.14	0.21 ± 0.06
H. convergens	0.01 ± 0.01	1.88 ± 1.61	0.19 ± 0.11	0.04 ± 0.03	0.03 ± 0.02	0.32 ± 0.23
H. parenthesis	0.00	0.05 ± 0.03	0.03 ± 0.03	0.00	0.02 ± 0.02	0.01 ± 0.00
C. septempunctata	0.00	0.10 ± 0.08	5.03 ± 3.73	0.72 ± 0.49	0.01 ± 0.01	1.53 ± 1.00
Other coccinellids	0.00	0.03 ± 0.02	0.12 ± 0.09	0.20 ± 0.18	0.00	0.09 ± 0.05

The number of 300-sweep samples taken from fields each year is in parentheses.

year to year (Table 2). Overall, the common damsel bug, *Nabis americoferus* Carayon (Hemiptera: Nabidae), was the most abundant aphid predator, followed in order by two coccinellids, *Hippodamia convergens* Guerin-Meneville and *Coccinella septempunctata* (L.), the common green lacewing, *Chrysoperla plorabunda* (Fitch) (Neuroptera: Chrysopidae), and another coccinellid *H. parenthesis* (Say). Other coccinellids such as *Coleomegilla maculata lengi, H. tredecimpunctata tibialis* (Say), *C. transversoguttata richardsoni* Brown, *Cycloneda munda* (Say), and *Adalia bipunctata* L. were captured in low numbers and were combined in a single category, "other coccinellids." Aphids in alfalfa fields were nearly all pea aphids (*Acyrthosiphon pisum* [Harris]). Aphid abundance varied greatly among years from a mean of 1.27 per 50 sweeps in 1988 to 96.5 per 50 sweeps in 1989.

Polynomial regression models describing the numerical response by adult predators to aphids in alfalfa fields were significant for *N. americoferus, C. plorabunda, H. convergens, H. parenthesis,* and *C. septempunctata* (Table 3). Occurrence of other species in samples was too sporadic for regression modeling. Even though regression models were significant, values of R^2 were low for most species. The exception was *C. plorabunda* for which $R^2 = 0.86$. Except for adult *H. convergens,* for which the model was linear, numerical response models included quadratic, cubic, or both powers of aphid abundance as predictor variables, indicating that rates of increase in predator abundance varied nonlinearly with aphid abundance. One or more regression parameters differed significantly among the three geographically separated alfalfa fields for each species of predator. For *H. parenthesis,* only the intercept differed among fields indicating that the overall abundance of this species differed among fields, but that the rate of increase in predator numbers in relation to aphid numbers was similar in the

Table 3. Statistics for multiple regression models of predator abundance versus aphid abundance for three geographically separated alfalfa fields sampled periodically during the growing season of each of 5 yr (1988–1992)

Life stage/Species	Regression statistic			Regression parameter[a,b]			
	F	*P*	R^2	Intercept	Aphids	Aphids^2	Aphids^3
Adult							
N. americoferus	5.17	<0.001	0.21	Yes (+)	—	—	Yes (+)
C. plorabunda	143.5	<0.001	0.86	No (+)	No (+)	Yes (+)	Yes (−)
H. convergens	4.13	0.002	0.18	No (+)	Yes (+)	—	—
H. parenthesis	6.69	<0.001	0.26	Yes (+)	No (−)	No (+)	No (−)
C. septempunctata	2.61	0.03	0.12	No (+)	—	Yes (−)	—
Immature							
N. americoferus	0.54	0.74	0.03	—	—	—	—
C. plorabunda	0.74	0.60	0.04	—	—	—	—
H. convergens	12.00	<0.001	0.38	No (+)	—	No (−)	Yes (+)
H. parenthesis	2.41	0.04	0.11	No (+)	—	Yes (+)	—
C. septempunctata	291.9	<0.001	0.93	No (+)	Yes (+)	Yes (−)	Yes (+)

—, If the regression parameter for a particular order term did not enter significantly into the overall regression model.

[a] If a regression parameter for a particular order term differed significantly ($P < 0.05$) among sites for a species a 'yes' is entered in the corresponding column, whereas if the parameter did not differ significantly among sites a 'no' is entered.

[b] The sign of the particular regression coefficient is in parentheses. When the sign of the regression coefficients for a particular order term differed among the three fields, the sign that predominated for the three fields is shown.

Table 4. Stepwise multiple regression models for aphid predator abundance and species diversity

Predator	Variables included[a]	R^2-model	R^2-covariables
Nabis americoferus	Crop density + (boundaries crossed)^2 − boundaries crossed − patch diversity^3	0.66	0.21
Chrysoperla plorabunda	Boundaries crossed + aphids + %crp − grass density	0.34	0.11
Hippodamia convergens	Patch diversity − %wetlands + broadleaf density^3 − %CRP^3	0.45	0.34
Hippodamia parenthesis	− %wooded + patch diversity − crop density^3	0.25	0.35
Coccinella septempunctata	Crop density + %wetlands + broadleaf density^3	0.41	0.33

Variables are listed in decreasing order of their contribution to the model R^2. The model R^2 indicates the contribution of all variables, excluding covariables. The contribution of covariables to the total R^2 is listed separately.

[a] Regression parameters are not listed, only the sign of the regression parameter is shown.

three fields. For all other species, the rate of change in predator abundance in relation to aphid abundance differed among fields.

Polynomial regression models for abundance of immature *N. americoferus* and *C. plorabunda* were not significant, suggesting a very limited or no reproductive numerical response to aphids by these species (Table 3). However, regression models were significant for the three species of Coccinellidae. Values of R^2 ranged from 0.11 to 0.93 for the three Coccinellidae species. As was true for adults of most species, numerical response models for immature Coccinellidae were second or third order polynomials. Furthermore, one or more regression parameters differed significantly among the three geographically separated fields, indicating that the reproductive numerical response by these predators varied with geographic location.

Vegetation and Landscape Effects on Predator Abundance. We observed a wide range of variation in the vegetation composition of alfalfa fields (Table 1). For example, canopy coverage by grasses ranged from 0 to 3.8 (mean = 1.0), whereas canopy coverage by alfalfa ranged from 2.5 to 6.0 (mean = 4.3). We also observed a wide range of variation in landscape variables (Table 1). For example, the percentage of CRP land in the nine 1.6-km^2 blocks incorporating a field ranged from 0 to 33.7% (mean = 5.2%), whereas the average number of boundaries crossed ranged from 3.8 to 11.6 (mean = 6.8).

The percentage of variation in predator abundance accounted for by covariables in multiple regression models ranged from 11 to 35% depending on the species of predator (Table 4). Covariables generally accounted for less of the variation in abundance than landscape and within-field variables did. An exception was the regression model for adult *H. parenthesis,* for which covariables accounted for 1.4 times more variation in adult abundance than predictor variables. Regression models accounted for 25–66% of the variation in adult predator abundance (Table 4). Landscape variables entered into stepwise regression models for each of the five species. Variables representing vegetation composition within fields also entered into models for each species. Aphid abundance was included in the regression model for abundance of *C. plorabunda.* Among landscape variables, Shannon's patch diversity index was most frequently incorporated in models, entering in models for three species. The number of boundaries crossed, percent CRP land, and percent wetlands each entered in models for two species, while percent wooded land entered the model for *H. parenthesis.*

Discussion

One objective of this study was to determine if the abundance of aphid predators in alfalfa fields was related to the abundance of aphids, as would be expected if the predators exhibited a numerical response to aphid density at the scale of individual alfalfa fields. Polynomial regression models indicated that adults of all predator species were more abundant in alfalfa fields when aphids were abundant than when they were not, demonstrating the existence of a numerical response. It should be noted that adults of *C. plorabunda* are not predaceous, but do feed on aphid honeydew (Principi and Canard 1984). Therefore, they may exhibit a numerical response to aphids, even though honeydew produced by the aphids is the resource to which they respond (Duelli 1980). Previous studies have demonstrated a numerical response by predators to aphids in alfalfa fields (Neuenschwander et al. 1975, Frazer et al. 1981, Evans and Youssef 1991, Giles et al. 1994), although some results from previous studies differed from ours. All of the above-mentioned studies observed that abundance of coccinellids was related to abundance of aphids in alfalfa fields. But Neuenschwander et al. (1975) and Evans and Youssef (1991) studied abundance patterns of Nabidae and found no relationship between nabid abundance and that of aphids. Neither study distinguished between adult and nymphal stages of Nabidae however, which may have reduced their ability to detect a numerical response if the response was only by adults as was the case in our study. Neuenshander et al. (1975) studied chrysopid abundance and found no relationship between abundance of adult or larval chrysopids and abundance of aphids. The studies of Neuenschwander et al. (1975) and Evans and Youssef (1991) differ from ours both in methodology and in geographic location to a great enough degree that it is difficult to discern the reasons for the differing results. For example, Neuenschwander et al. (1975) and Evans and Youssef (1991) did not report the species of Nabidae they encountered, and the species may or may not have been *N. americoferus.* Furthermore, the cultural practices used in alfalfa production in their studies may or may not have been similar to those used in eastern South Dakota. Cultural practices such as cutting have a substantial impact on survival and dispersal of insects in alfalfa fields, and the impact of cultural practices on survival and dispersal differs among taxa (Richards and Harper 1978, Harper et al. 1990, Schaber et al. 1990, Schaber and Entz 1994). Duelli (1980) observed strong appetitive flight by adult *C. plorabunda* to habitat patches with aphid honeydew, and found that immigration and emigration rates of adults from habitats was strongly dependent on the presence of aphid honeydew. Duelli's (1980) results suggest that a relationship between adult *C. plorabunda* and aphid abundance should often be expected to occur.

In the current study, the percentage of variation in predator abundance accounted for by aphid abundance in numerical response models (values of R^2 for regression models) was very low for most predators, indicating that factors other than the abundance of prey played an important role in determining the number of predators in alfalfa fields. Furthermore, parameters of numerical response models differed significantly among geographically separated alfalfa fields indicating that the numerical response by predators was dependent on the geographical location of a field. The explanation for both observations lies partially in the roles that the vegetation within a field habitat and in the surrounding landscape play in determining predator distribution and abundance in space. The size and species composition of the pool of predatory insects available to colonize a particular habitat and the proportion of that pool that actually colonizes the habitat vary spatially as the result of population processes that occur in the adjacent landscape (Honek 1982, Liss et al. 1986). Multiple regression models demonstrated the importance of the composition and structure of the landscape matrix and of the composition of the plant community within alfalfa fields in determining the abundance of aphid predators in them.

Even though variables describing landscape composition and patch size were very general, with no known relation to the ecological requirements of the aphid predators, they explained a higher proportion of the variation in predator abundance in alfalfa fields than aphid abundance did. It is probably not appropriate to interpret the results as indicating that landscape and habitat variables were more important than aphids in determining the abundance of aphid predators, because the variables were measured with different levels of precision. For example landscape composition was measured without sampling error because all the land in the 4.8 km^2 of land surrounding each field was included. However, habitat variables and aphid abundance were subject to both sampling and measurement errors. Even with that limitation, it is clear that factors other than aphid abundance play an important role in determining the abundance of predators in alfalfa fields.

The coccinellids *H. convergens*, *H. parenthesis*, and *C. septempunctata* exhibited a reproductive numerical response to aphids in alfalfa fields. However, neither *C. plorabunda* nor *N. americoferus* exhibited evidence of a reproductive numerical response to aphids. This observation may be related to the degree of prey specialization of the various predators. Most coccinellids that occur in alfalfa fields in eastern South Dakota are aphid specialists, and although they eat a variety of prey other than aphids, and some eat pollen and nectar, aphids are an essential food for optimal survival and reproduction (Hodek and Honek 1996). However, chrysopids and nabids feed on a wide variety of small soft-bodied arthropods besides aphids, including the eggs and larvae of Lepidoptera and Diptera (Principi and Canard 1984, Lattin 1989). The absence of a detectable reproductive numerical response by nabids and chrysopids may reflect the more general feeding habits of these predators compared with coccinellids.

Honek (1982) observed that the abundance of adult Coccinellidae in agricultural fields depended on landscape position in the early spring, but not later in the growing season. This was presumably related to the close location of some fields to wooded habitats, which allowed coccinellids emigrating from these overwintering sites to colonize fields early in the growing season. Later in the growing season, when coccinellids had presumably dispersed more homogeneously across the landscape, no landscape position effect was observed. The implication of Honek's (1982) study is that landscape effects on coccinellids are primarily restricted to availability of overwintering habitat and that these effects are ephemeral. Elliott et al. (1998) observed an effect of seminatural habitats (including woods) on coccinellid abundance in spring wheat fields. However, because sampling in the fields was confined to spring it remained unknown whether the distribution of spatially varying resources for coccinellids other than overwintering habitat affected their abundance in agricultural fields. Colunga-Garcia et al. (1997) observed that the presence of uncultivated habitats in the surrounding landscape affected the number of species of Coccinellidae in agricultural fields, but their study did not address the seasonal nature of these effects because the species abundance data on which analyses were based were averages over the entire growing season. Our regression analyses, which were based on individual samples of beetles from alfalfa fields made during midsummer, a time when most beetles from the previous overwintering generation would already have died (Elliott and Kieckhefer 1990), demonstrates that landscape effects can persist during summer, and suggests that features of the landscape other than overwintering habitat play a role in coccinellid population dynamics.

In hindsight it seems obvious that features of the habitat and landscape would influence populations of predatory insects in ephemeral agroecosystems like alfalfa. However, it was not obvious that the composition of vegetation in an alfalfa field and in the surrounding landscape might be as important as prey density in determining the abundance of predators in the field. Our study highlights the importance of a comprehensive approach to ecological studies of predatory insects to determine their potential as biological control agents. Such an approach may uncover ways to improve the effectiveness of these predators in biological control of aphids by manipulating the habitat within fields and in the surrounding landscape.

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